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Research paper

Risk of spread of tomato yellow leaf curl virus (*TYLCV*) in tomato crops under various climate change scenarios

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ABSTRACT

Species distribution models (SDMs) are valuable for the information they provide to reduce the potential negative effects of climatic factors on agricultural production systems. Such information may be used to prevent the entry and spread of invasive species in new areas, as well as to monitor regions with current occurrence. This is the first study of Tomato yellow leaf curl virus (*TYLCV*) global distribution, focusing on the risk of this disease in areas projected to be suitable for open field tomato (*Solanum lycopersicum*) and for whitefly (*Bemisia tabaci* - biotypes B and Q). *TYLCV* (Begomovirus) is an important virus transmitted by *B. tabaci* and poses a risk to *S. lycopersicum* cultivation worldwide. Despite the importance of *TYLCV*, the potential impact of climate change on the global distribution of *TYLCV* in agricultural crops remains unstudied. The aim of this study was to identify the invasion risk levels for *TYLCV* in areas optimally conducive for open field tomato cultivation and suitable for *B. tabaci* (biotypes B and Q) under projected climate changes for the years 2050 and 2070 using MaxEnt and the Global Climate Model (HadGEM2_ES, MIROC5 and CCSM4) under four scenarios (RCPs 2.6, 4.5, 6.0, and 8.5). Our results show that large regions are projected to be suitable for *TYLCV* in areas of suitability for *B. tabaci* and optimal for open field tomato cultivation. In the predictions, most areas with optimal conditions for *S. lycopersicum* and suitable for *B. tabaci* will be under medium suitability for *TYLCV* under climate change scenarios. This research may be useful to design strategies to prevent the introduction and establishment of *TYLCV* where the occurrence has not yet been reported.

1. Introduction

Tomato yellow leaf curl virus (*TYLCV*) (family Geminiviridae, genus *Begomovirus*) is one of the most important viruses affecting cultivated tomatoes globally (Czosnek and Laterrot, 1997). The *TYLCV* virus was first reported in the Middle Eastern Mediterranean areas and has spread to many tropical and subtropical regions around the world (including the Mediterranean Basin, the Far East (Asia), Caribbean, Australia, North and Central America and South America – so far only in Venezuela) (Czosnek and Laterrot, 1997; Kil et al., 2016; Lefeuvre et al., 2010; Navas-Castillo et al., 2011; Ning et al., 2015; Zambrano et al., 2007; Zhang et al., 2009). Recently, *TYLCV* has been reported to be seed-transmissible (Kil et al., 2016, 2017, 2018), but most transmission occurs due to the vector *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae), especially by the B and Q biotypes (Pan et al., 2012). *B. tabaci* is one of the most invasive insect pests of vegetables and other crops worldwide and can be spread solely by the adult stages of whiteflies (Ning et al., 2015; Pakkianathan et al., 2015). In this study, we considered the occurrences of these two biotypes (B and Q) to undertake the model, since they are shown to be similar in various aspects, such as climate requirements, the fact that the biotypes B and Q have strongly suppressed the other biotypes, and because these biotypes are considered the most invasive and important to tomato crops (Pan et al., 2012; Ramos et al., 2018).

The virus has the potential to cause large economic losses in crops, even annihilating a complete production cycle, depending on the phase of crop development at the time of infection (Pan et al., 2012). This virus is primarily known for its infestations of the tomato, *Solanum lycopersicum*, a vegetable crop of global economic importance, especially in tomato producing countries, such as China, Italy, Egypt, Iran, Spain, India, the United States and Turkey ((FAOSTAT), F.S.D., 2017).

After infection, the tomato plants may show some symptoms, such

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as severe stunting, marked reductions in leaf size, interveinal chlorosis, mottling, upward cupping, and abscission of flowers and the fruit, if produced at all, are small, dry and unfit for sale (Inoue-Nagata et al., 2016; Lefeuvre et al., 2010; Papayiannis et al., 2010). The severity of infection in the population of tomato plants is linked with the level of the *B. tabaci* populations, the vector for *TYLCV* (Czosnek and Ghanim, 2011). In this context, the best way to prevent losses due to *TYLCV* disease is to prevent its establishment in areas where tomato cultivation is important. To achieve this, it is important to consider the use of genetic resistance in the plant host, avoid the trade of infected host plants and seedlings, and control *B. tabaci* in fields, greenhouses, seedling nurseries and the surrounding vegetation (Hanssen et al., 2010).

Climate is a major factor affecting the global distribution of a species (Elith and Leathwick, 2009a; McDowell et al., 2014). Studies of the climate effects on the future distribution of plant diseases have advanced and attained significant relevance in recent years (Galdino et al., 2016; Shabani and Kumar, 2013). Climatic parameters, particularly temperature and precipitation, play a significant role in the development of diseases and in the interactions of vectors, crops, and diseases, since alterations of climate may alter the conditions for infectious disease organisms, plant hosts and vectors (Daugherty et al., 2017; Patz et al., 1996). *TYLCV* infection occurs most frequently at high temperatures and is found to be the most destructive in many tropical and subtropical regions at higher temperatures (Lapidot et al., 2000, 2006). The infection of the plants is also enhanced by the presence of whiteflies (*B. tabaci*), infected transplants and weedy fields with many alternative hosts. In addition, the insect vector (*B. tabaci*) also prefers high temperatures (Morales and Jones, 2004). Climate change will clearly affect the pathogen-host interaction, and altered conditions may contribute more favorably to the transportation/relocation, introduction, establishment, and subsequent spread of a virus or its vector in previously unfavorable regions.

Studies using species distribution models (SDMs) provide the data on which to base decisions and plan strategically to reduce the potential negative impact of changing climatic factors, such as temperature and precipitation, on agricultural production systems (Crespo-Pérez et al., 2015). This is particularly applicable to predict the effects of global warming on economically important crops, such as tomatoes, as well as the altered risk of insect and disease attacks (Jarošík et al., 2015). Climatic models are considered an important tool to determine the sensitivity of species, such as plants, invasive insects, and diseases, to climate alteration (Adams et al., 1990; Shabani and Kumar, 2013). Modeling offers a technique to simulate future climates using different climate change scenarios (Kriticos et al., 2012) based on the tolerance limits of the species under the current climate range. Studies based on modeling can predict potential distributions and abundance under future climate scenarios, which are vital to develop management strategies and highlight the interactions between environmental variables, such as temperature and precipitation, and species, as well as the principal abiotic factors that may affect the introduction and establishment of some species (Pearson and Dawson, 2003; Soberon and Peterson, 2005).

Despite the impact of *TYLCV* and the substantial body of research on the interaction of *B. tabaci* as an insect vector, tomato as its principal host and *TYLCV* as the pathogen, there have been no studies on the potential impact of climate change on the global distribution of *TYLCV* in agricultural crops, particularly in tropical and subtropical regions. In light of this absence of research, we modeled the invasion risk of *TYLCV* in areas suitable for open field *S. lycopersicum* cultivation and for *B. tabaci* under climate change under four future scenario Representative Concentration Pathways (RCP) (RCPs 2.6, 4.5, 6.0, and 8.5). Note that model projections for *S. lycopersicum* and *B. tabaci* (biotypes B and Q) have been undertaken in the past (Ramos et al., 2018), but projections have only been made for RCP 4.5. In this study, we extend the modeling for these two species to RCP 2.6, 6.0, and 8.5 and model future projections for *TYLCV* for all four RCPs for 2050 and 2070. We overlaid these onto the predicted future distributions of *S. lycopersicum* and *B. tabaci* (biotypes B and Q) to ascertain the areas optimally conducive for *S. lycopersicum* cultivation and suitable for *B. tabaci* (biotypes B and Q) but at different risk levels for *TYLCV*. We also identified climatic factors associated with *TYLCV* distribution and describe the implications of these for both the present and future in terms of successful tomato crop production and the design of more efficient strategies to control the spread of *TYLCV* in open-field tomato farming.

2. Material and methods

2.1. Current distribution of TYLCV, S. lycopersicum and B. tabaci

The data for the three species included in this research were collected from GBIF.org, 2017, EPPO, the Geminivirus database (http://geminivirus.org:8080/geminivirusdw/) (Silva et al., 2017), and other references (Supplementary Material-1) (for *TYLCV:* 134 locations, for *S. lycopersicum:* 186 occurrences and *B. tabaci* (biotypes B and Q)*:* 627 occurrences). We crosschecked all the countries worldwide and included only locations with open field tomato cultivation. Eventually, the *TYLCV* records were reduced to 118, *S. lycopersicum* to 177 occurrences and *B. tabaci* to 421 occurrences after applying spatial filtering using spThin, an R package that reduces spatial autocorrelation (Aiello-Lammens et al., 2015) (Supplementary Material-1.1). We selected this method since it retains as many localities possible and is more effective than other methods in reducing spatial autocorrelation (Boria et al., 2014). The filtered occurrence data points were > 5 km apart (Boria et al., 2014; Veloz, 2009). This distance was selected to restrict each cell to only one occurrence point since we used ~5-km spatial resolution climatic data in the model.

2.2. Environmental data layers

Initially, we considered 19 variables of temperature and precipitation (Table 1). These bioclimatic parameters were obtained from the WorldClim dataset (http://www.worldclim.org/) (Hijmans et al., 2005). The data layers used had 2.5 min spatial resolution (~5 km), a resolution of sufficiently high quality to support climatic variables at a global scale since they cover all global land surfaces with great resolution and accuracy. High spatial resolution climate data is often necessary for ecological and modeling studies (Daly, 2006; Elith and Leathwick, 2009b). The average temperature and precipitation data covering 1960–1990 and other parameters (Table 1) were drawn from the seasonal variables and climatic extreme indices (Hijmans et al., 2005). The average temperature, precipitation, seasonal variables, and climatic extreme indices were used.

We used the SDM tools in the ArcGIS software to remove variables with high correlation, and only one variable from a group with correlation was included based on the Pearson correlation coefficient, $r \geq |0.75|$ (Table S1). In addition, these variables are considered biologically more meaningful for the species (Hijmans et al., 2005). Temperature and precipitation are the most important for the growth and development of *B. tabaci* (Ramos et al., 2018), and disease incidence such as *TYLCV* (Rai et al., 2001; Lee and Denlinger, 2010). In this study, only six bioclimatic variables were selected based on realistic biological relevance to the species (*TYLCV*, *S. lycopersicum* and *B. tabaci*) (Hijmans et al., 2005; Ramos et al., 2018) (Table 1; Table S1).

2.3. MaxEnt software - model development and validation

MaxEnt, maximum entropy-based model algorithm, version 3.3.3 k (Phillips et al., 2006), was used to predict the global distributions of *TYLCV*, *S. lycopersicum* and *B. tabaci*.

MaxEnt was chosen because it uses species presence and background data (absence data are not needed), and it is appropriate for

Table 1
Environmental variables considered in the *TYLCV* niche models and the average percent contribution of environmental variables in the *TYLCV* distribution model. The values were averaged across 10 replicate runs. General statistics were calculated using all occurrences (n = 133). (Min = minimum, Max = maximum, and SD = standard deviation).

Variable	Percent contribution	Permutation importance	Min.	Max.	Mean	SD
Annual mean temperature (bio1; °C)	60.2	56.5	8.5	29.1	19.5	5.2
Temperature annual range (bio7; °C)	14.5	8.6	7.3	45.4	26.8	8.9
Mean diurnal range in temperature (bio2; °C)	14.1	16.3	5.2	18.4	10.9	2.7
Precipitation seasonality (CV) (bio15)	6.2	8.6	27	159	73.8	32.3
Precipitation of the driest month (bio14; mm)	2.9	4.3	0	221	22.1	30.5
Mean annual precipitation (bio12; mm)	2.2	5.7	7	3146	890.5	710.2
Isothermality (bio3)	–	–	23	82	44.3	16.2
Temperature seasonality (SD × 100) (bio4)	–	–	533	12,234	5597	2985
Maximum temperature of the warmest month (bio5; °C)	–	–	16.1	46.0	32.8	4.3
Minimum temperature of the coldest month (bio6; °C)	–	–	−16.3	21.9	6.0	8.8
Mean temperature of the wettest quarter (bio8; °C)	–	–	7.3	31.4	21.3	6.3
Mean temperature of the driest quarter (bio9; °C)	–	–	−8.2	35.4	17.9	10.6
Mean temperature of the warmest quarter (bio10; °C)	–	–	11.5	35.4	26.5	3.5
Mean temperature of the coldest quarter (bio11; °C)	–	–	−8.2	26.7	12.2	85.0
Precipitation of the wettest month (bio13; mm)	–	–	2	666	165	119.8
Precipitation of the wettest quarter (bio16; mm)	–	–	4	1878	419.7	318.3
Precipitation of the driest quarter (bio17; mm)	–	–	0	736	79.2	101.6
Precipitation of the warmest quarter (bio18; mm)	–	–	0	1454	307.4	147.1
Precipitation of the coldest quarter (bio19; mm)	–	–	0	1210	147	171.2

Bold font indicates variables in the final model. Source of the data: WorldClim (http://www.worldclim.org/bioclim; Hijmans et al., 2005).

small sample sizes (Kumar and Stohlgren, 2009; Pearson et al., 2007). MaxEnt is a machine learning method that predicts the potential distribution of species based on maximum entropy (Phillips et al., 2006). This method is less sensitive to small sample sizes using small sampling and background data (Kumar et al., 2009, 2014a,b; Kumar and Stohlgren, 2009). This program is most suited to our research based on the presence-only data available for the pathogen and host (Phillips et al., 2006). MaxEnt generates a suitability index of the species ranging from 0 (for unsuitable) to 1 (for optimum suitability) per grid cell.

Background data was generated using the kernel density layer and Hawths Tools extension (Beyer, 2004). The background points were placed in the parts of the world that have been accessible to the species via dispersal over relevant periods of time. We considered terrestrial Ecoregions (Mediterranean) basin as well as in tropical and subtropical regions to delimitate the area.

A sampling bias was generated in that the data were collected from external sources, in which we had no control of the sampling process. SDMToolbox was employed to generate the bias surface using a kernel density estimate (Brown, 2014). The bias surface will result in a raster where cells with lower values will represent places with lower bias (Galdino et al., 2016; Phillips et al., 2006). The bias surface was used to establish sampling intensity and potential sampling bias (Jarnevich et al., 2015).

We made adjustments to the MaxEnt default settings combining different feature types, and the regularization multiplier (RM) to find the best model for the species *TYLCV*, *S. lycopersicum* and *B. tabaci* (Jarnevich et al., 2015; Kumar et al., 2014b; Merow et al., 2013). We first combined different sets of MaxEnt features: linear [L], quadratic [Q], product [P], threshold [T], and hinge [H] (Table 2) with the RM. The RM was used to control the number of parameters and consequently the model complexity (Elith et al., 2011; Merow et al., 2013). We used three values of RM (1.0; 1.5 and 2.0) for the species (Table 2). Models are very restricted when the RM is below 1 and is inappropriate for global predictions. An RM value > 1 generates models with a broader potential distribution (Phillips et al., 2006).

To eliminate extrapolations from the environmental range, we used the MaxEnt 'fade-by-clamping' (Owens et al., 2013). The 'jackknife' technique and percentage contribution were used to estimate the importance and contribution of the environmental variables. Response curves were generated in MaxEnt, and we chose only the environmental variables that represented strong relationships between the probabilities of the presence for each species with each environmental predictor. All the response curves were evaluated in terms of providing biological logic. This indicates that the probability of the presence of each species does not display many ups and downs as the precipitation or temperature increases. This is not what we expect to occur with living organisms, and those that failed this test were not considered for further evaluations.

To compare the performance of the models, we calculated the Bayesian Information Criterion (BIC) using ENMTools for the selection of the best model (Warren et al., 2010). We chose this criterion because it has a higher penalty for the model complexity than the Akaike Information Criterion (AIC). Similar to AIC a smaller BIC value means a 'better' model (Kumar et al., 2015). In adittion, we selected test sensitivities of 0% and 10% training Omission Rates (OR) (Kumar et al., 2014a, 2015; Liu et al., 2013) and the AUC_{cv} (area under the receiver operating characteristic [ROC] curve) (Peterson et al., 2008). To calculate the AUC_{cv} and OR, a 10-fold cross-validation was run in MaxEnt. AUC_{cv} was also used present from the background data. When the AUC_{cv} value is 0.5, it indicates that model predictions are no better than random; values below 0.5 are less than random; values between 0.5 and 0.7 indicate poor performance; values between 0.7 and 0.9 indicate moderate performance, and values > 0.9 indicate high performance (Peterson et al., 2011). In the case of the OR, the expected value at 0% training is 0, and at 10% it is 0.10; models show poor performance when the value exceeds the expected omission rates (Boria et al., 2014). Model ranking was based on 10% training OR, 0% training OR, and AUCcv in this order, respectively (Kumar et al., 2014a; Liu et al., 2005; Merow et al., 2013). ArcGIS 10.3.1 software was used to extract the MaxEnt outputs to project areas suitable for open field tomato cultivation under varying levels of risk of invasive *TYLCV* under future scenarios.

2.4. Global climate models and climate change scenarios

To model the potential distributions, for each species (*TYLCV* as a pathogen, *S. lycopersicum* as the host and *B. tabaci* as an insect vector), we chose three different Global Climate Models (GCMs) for the years 2050 and 2070 (all the results for *S. lycopersicum* and *B. tabaci* are addressed in the Supplementary Material-3): the first one, HadGEM2_ES, the second one MIROC5, and the third and last one CCSM4. They were selected to run under four Special Report on

Table 2
Summary of the performance statistics of the *TYLCV* MaxEnt models. The best model is highlighted in bold.

ModelRank	Variables	MaxEnt settings		Test AUC_{cv} (± SD)	OR		AICc	BIC
		Features	RM		0%	10%		
1	bio1,bio2,bio7, bio12, bio14, bio15	LQP	1.0	0.887 ± 0.036	0.0258	0.1114	3008.64	3147.19
2	Same as above	LQP	2.0	0.883 ± 0.038	0.0341	0.1189	3109.22	3147.75
3	Same as above	LQH	2.0	0.883 ± 0.035	0.0083	0.1364	3102.19	3148.01
4	Same as above	LQH	1.5	0.886 ± 0.033	0.0174	0.1379	3017.86	3148.77
5	Same as above	LQP	1.5	0.882 ± 0.040	0.0348	0.1277	3110.68	3151.18
6	Same as above	LQPT	1.5	0.882 ± 0.036	0.0265	0.1689	3102.76	3154.09
7	Same as above	LQPH	1.5	0.883 ± 0.035	0.0174	0.1477	3106.72	3156.05
8	Same as above	LH	2.0	0.886 ± 0.034	0.0167	0.1455	3127.90	3172.68
9	Same as above	LQPTH	1.5	0.886 ± 0.036	0.0364	0.1310	3118.78	3177.07
10	Same as above	LQPH	1.0	0.880 ± 0.039	0.0523	0.1932	3118.67	3177.41
11	Same as above	LH	1.0	0.886 ± 0.034	0.0174	0.1735	3211.24	3211.24
12	Same as above	LQPT	1.0	0.879 ± 0.033	0.0614	0.2091	3172.86	3235.91

Note: Variable full names (see Table 1). L, Q, P, T and H are linear, quadratic, product, threshold and hinge features, respectively. RM is the regularization multiplier, and SD is the standard deviation. OR is the test omission rate. Test AUC_{cv} is the MaxEnt 10-fold cross-validation Area Under the ROC curve. AIC_c is Akaike information criterion and BIC is Bayesian information criterion.

Emissions Scenarios (SRES) scenarios, RCP 2.6, RCP 4.5, RCP 6.0 and RCP 8.5. The selected model HadGEM2-ES is a product of the Hadley Center Global Environmental Model associated cycle of the fifth phase of the CMIP5 (http://www.ipcc.ch/report/ar5/wg1/) (Taylor et al., 2012). This model incorporates interactive land and ocean carbon cycles and dynamic vegetation, offering the option to prescribe either atmospheric CO_2 concentrations or anthropogenic CO_2 emissions with simulated CO_2 concentrations. With a CO_2 doubling rate of approximately 4.68 °C, it ranks near the top of the CMIP5 range (Andrews et al., 2012; Dike et al., 2015).

The model MIROC5 (Model for Interdisciplinary Research on Climate) is a product of the Atmosphere and Ocean Research Institute (The University of Tokyo), the National Institute for Environmental Studies, and the Japan Agency for Marine-Earth Science and Technology (Japan) and projects moderate warming not exceeding 3 °C. The MIROC5 employs a prognostic treatment for the cloud water and ice mixing ratio, as well as the cloud fraction, considering both warm and cold rain processes and reveals an equilibrium climate sensitivity (Watanabe et al., 2010).

The model CCSM4 is a global climate model consisting of atmosphere, land, ocean, and sea ice components. CCSM4 shows improvements in the annual cycle of air temperature for Alaska and India. The biggest surface air temperature bias in CCSM4 is a + 2° to + 4 °C annual mean warm bias over Europe and western Asia. The current air temperature within urban areas is warmer than the surrounding rural areas by 1–2 °C, and it is increasingly suited for studies of the role of land processes in climate change (Lawrence et al., 2012).

Our study focuses on future predictions under four different scenarios. The four RCPs represent “low” (RCP 2.6), “medium” (RCP 4.5 and RCP 6.0) and “high” (RCP 8.5) scenarios featured by the radiative forcings of 2.6, 4.5, 6.0 and 8.5 W m^{-2} by 2100, respectively. The RCPs offer an extensive range of potential changes in future anthropogenic greenhouse gas (GHG) emissions (Long-term Climate Change, 2014). Across all the RCPs, the global mean temperature is projected to increase in the range by 0.3 to 4.8 °C by the late 21st century (IPCC, I.P.o.C.C., 2014).

2.5. Determining TYLCV risk levels and the combination of the model outputs for TYLCV, S. lycopersicum and B. tabaci

The Maximum Test Sensitivity Plus Specificity (MTSPS) threshold was chosen to extract from the projected future distributions of three species. We could determine suitability classes for *TYLCV, B. tabaci* and *S. lycopersicum* from the MTSPS (showing which areas would be optimal for open field tomato crops and suitable for *B. tabaci* and would be at high, medium or low risk levels for *TYLCV)*. This threshold was chosen to use the projected future distributions of each species (*TYLCV, B. tabaci* and *S. lycopersicum*) to demonstrate which areas would be at invasion risk, using the categories of highest, medium and lowest risk. This threshold was chosen since it is considered to be simple and effective to the average probability/suitability approach and to define the class of suitability with accuracy (Liu et al., 2005). To overlay, “optimal conditions” were defined as areas of medium or high suitability for *S. lycopersicum* in that these corresponded to areas that either are or would be of high suitability based on the climate conditions to grow and develop tomato crops. For projections for the three species, as well as for the overlaying to determine the risk levels of *TYLCV* in areas with optimal conditions for tomato crops and suitable for *B. tabaci,* we used four suitability classes (unsuitable: 0-MTSPS; low: MTSPS-0.5; medium: 0.5–0.7 and high: 0.7–1.0).

3. Results

The annual mean temperature (bio1; °C), temperature annual range (bio7; °C), mean diurnal range in temperature (bio2; °C), precipitation seasonality (CV) (bio15), precipitation of the driest month (bio14; mm) and mean annual precipitation (bio12; mm) were the climatic variables that most contributed to *TYLCV* distribution (Table 1). Therefore, to the observed occurrences, *TYLCV* occurs in areas with a mean annual temperature of 19.5 °C and an annual precipitation range of 7–3146 mm with a mean of 890.5 mm (Table 1). The annual mean temperature also showed the highest permutation importance (56.5%), followed by the mean diurnal range in temperature (16.3%), temperature annual range (8.6%), precipitation seasonality (8.6%), mean annual precipitation (5.7%), and precipitation of the driest month (4.3%) (Table 1).

All the performance statistics of the *TYLCV* MaxEnt models are provided in Table 2. The average BIC values ranged from 3147.10 to 3235.91 and AICc values ranged from 3008.64 to 3211.24. The average AUC_{cv} values ranged from 0.879 to 0.887 (Table 2). These models displayed low test omission rates with values varying from 0.0083 to 0.0614 at a 0% training omission rate and from 0.1114 to 0.2091 at 10% (Table 2). The best model comprised six environmental variables and Linear, Quadratic, Product (LQP) features (Table 2).

The Jackknife test of the importance of variables indicated that the mean annual temperature had more information than the other variables (Fig. S1). The highest probability for the presence of *TYLCV* was found in localities with a mean annual temperature of 19–20 °C. The probability of *TYLCV* infection was higher in areas with lower precipitation, decreasing with the increase in precipitation. The probability of the *TYLCV* presence was also higher in areas of low mean diurnal

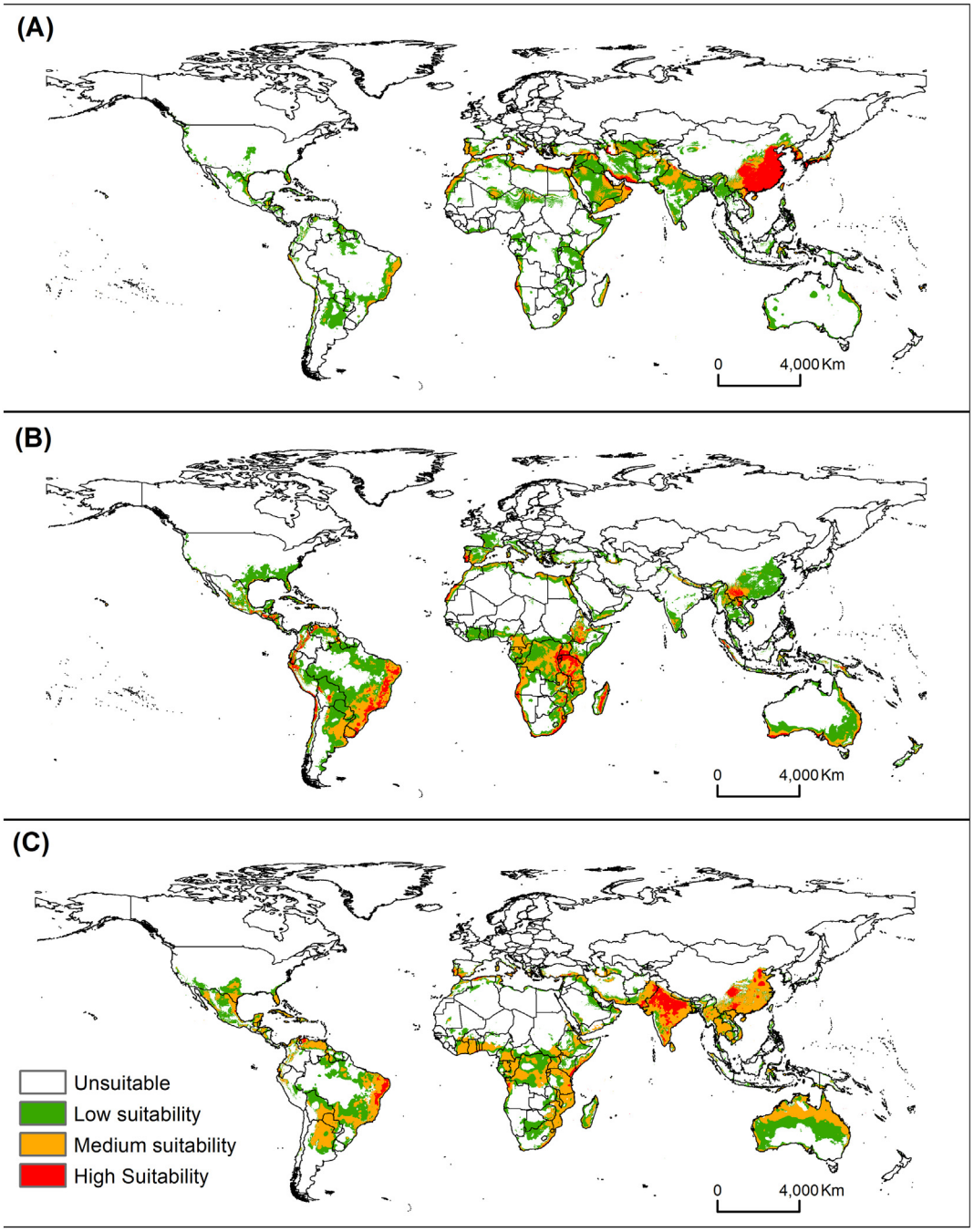

Fig. 1. Habitat suitability under current climatic conditions using the MaxEnt model, (A) *TYLCV*, (B) *S. lycopersicum* (Ramos et al., 2018) and (C) *B. tabaci* (Biotype B and Q) (Ramos et al., 2018).

temperature range (Response curves, Fig. S2 – Supplementary Material-3).

Comparing the MaxEnt global climate suitability model with a global distribution of *TYLCV* (Fig. 1A, S3A - Supplementary Material-2), open field *S. lycopersicum* (as a host) (Fig. 1B, S3B), and *B. tabaci* distribution (as an insect vector) (Fig. 1C, S3C - Supplementary Material-2) shows consistency with the current global distributions of their known occurrences. Climatic conditions suitable for *TYLCV* are projected for many regions globally. Although there are areas in South America, which are under risk for *TYLCV*, this virus species has not yet been reported from those areas (Figs. 1A, 2, Figs. S3, S4, S5, S17, S18 and S19 - Supplementary Material-2). The tomato model also displayed global agreement between known occurrences and projections (Fig. 1B, Figs. S3, S14, S15, S16, S17, S18 and S19 - Supplementary Material-2). The current and projected climate results for *TYLCV* indicate low, medium and high suitability areas in Europe, Asia, north Central and South America, and Africa (Figs. 1A, 2, Figs. S4, S5, 3, S6 and S7 - Supplementary Material-2).

3.1. Projected results from the model for TYLCV under various climate change scenarios

According to the projected scenarios for 2050 and 2070, many areas in the world, such as South America (e.g., Argentina and some areas along the coastlines of Brazil), North America (the United States), Africa (along the coastlines of the continent) and the south of Europe, are projected by the HadGEM2_ES, MIROC5 and CCSM4 models to sustain suitability for *TYLCV* (Figs. 2, 3, Figs. S4, S5, S6 and S7-

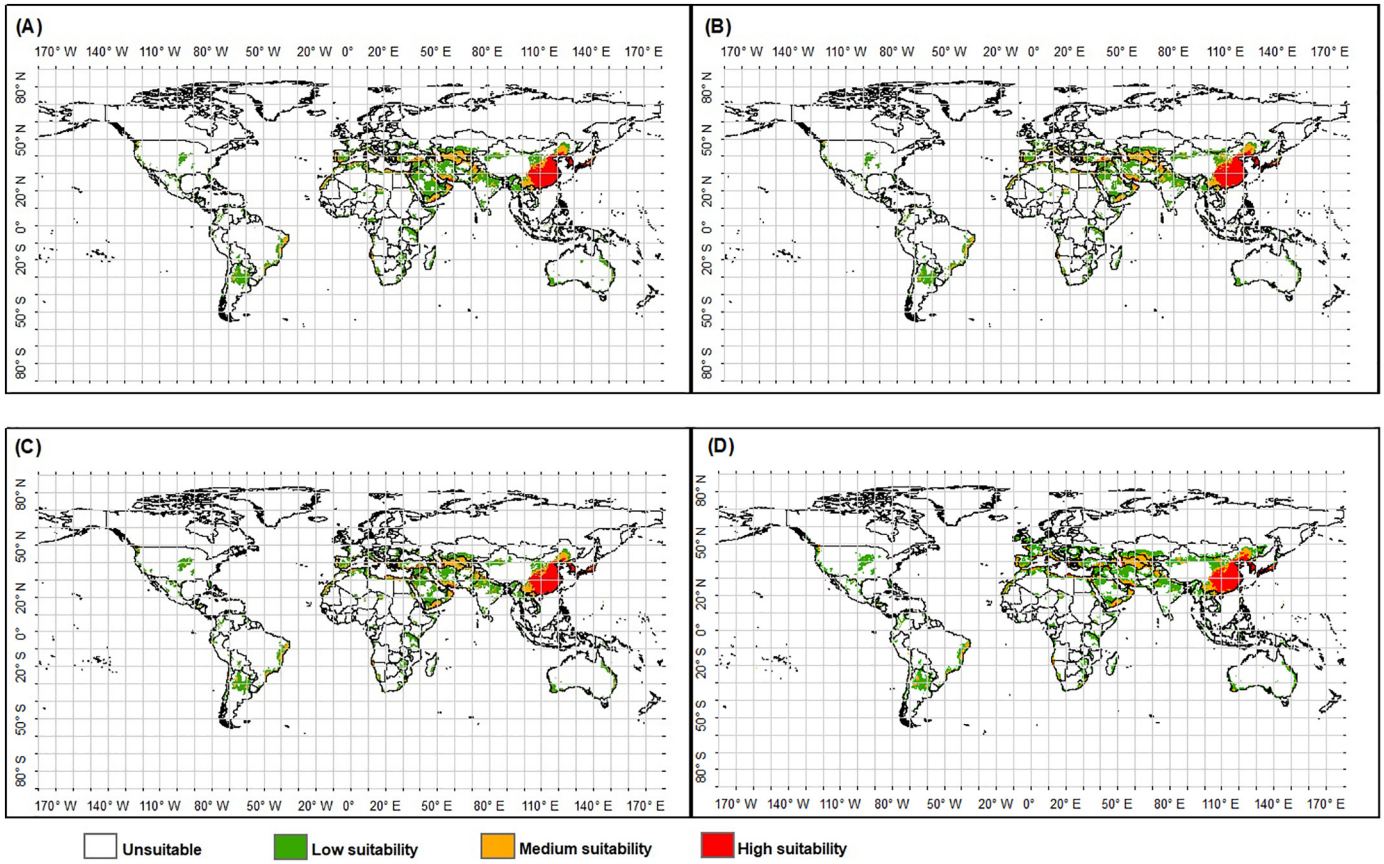

Fig. 2. Habitat suitability under future climatic conditions (2050) for *TYLCV* using the HadGEM2_ES - MaxEnt model running four scenarios (A) RCP 2.6, (B) RCP 4.5, (C) RCP 6.0 and (D) RCP 8.5.

Supplementary Material-2). The model further demonstrates that this suitability will increase for 2050 and 2070 in a northern direction in Europe (in countries, such as Spain, Italy, France, Germany and Hungary), Asia (northern China), North America (some sites in the United States), and a decrease in Asia (India) and Africa. However, suitability will decrease in South and Central America, Africa, Asia (India) and Iran (Figs. 2, 3, Figs. S4, S5, S6 and S7 - Supplementary Material-2).

When the performance of the three future projections is compared (HadGEM2_ES, MIROC5 and CCSM4), all the GCMs demonstrate suitability for the same regions at the global scale (in all continents) with the increase in the northern direction in Europe, Asia and America. The HadGEM2_ES seems to show more restrictions (lower areas under low suitability) than the others in all the RCPs compared to the MIROC5 and CCSM4 in Africa, South America and Australia (countries located in the southern hemisphere).

It should be noted that, while there are not many differences among the scenario (RCP 2.6, RCP 4.5, RCP 6.0, RCP 8.5) projections, RCP8.5 shows larger areas under low suitability (e.g., the United States, northern Europe and northern China) compared to the other scenarios.

3.2. Projected results from the model for tomato crops under various climate change scenarios

According to the projected scenarios for 2050 and 2070, many areas on all the continents (Americas, Africa, Asia, Europe, and Oceania) are projected by the HadGEM2_ES, MIROC5 and CCSM4 models to decrease in suitability for tomato crops (Figs. S14, S15, S16, S17, S18 and S19 - Supplementary Material-2). However, the model demonstrates that suitability will increase in a northern direction in some European countries (e.g., Spain, Italy, France, Germany and Hungary) and will be maintained in other areas (e.g., along the coastlines of Brazil, south of Europe and west of Africa) for this host species for 2050 and 2070. Again, although there are not many differences between the scenarios (RCP 2.6, RCP 4.5, RCP 6.0, RCP 8.5), RCP 6.0 and RCP 8.5 show a larger decrease in areas (e.g., Africa, South America, Australia and China) suitable for open field tomato crops above the general decline in suitability for 2050 and 2070 (Figs. S14, S15, S16, S17, S18 and S19 - Supplementary Material-2).

3.3. Projected results from the model for B. tabaci under various climate change scenarios

According to the projected scenarios for 2050 and 2070, many areas on all the continents in the world (Americas, Africa, Asia, Europe, and Oceania) are projected by the HadGEM2_ES, MIROC5 and CCSM4 models to maintain suitability for *B. tabaci* (Figs. S8, S9, S10, S11, S12 and S13 - Supplementary Material-2). However, this model demonstrates that suitability for this insect vector species will increase for 2050 and 2070 in European countries (Spain, Italy, France, Germany and Hungary), North America (United States) and decrease in parts of South America, India and Australia. While there are few differences between the scenarios (RCP 2.6, RCP 4.5, RCP 6.0, and RCP 8.5), RCP 8.5 shows a greater decrease in some areas (e.g., Africa and India) of suitability for *B. tabaci* but an increase in others (e.g., the United States and Europe) (Figs. S8, S9, S10, S11, S12 and S13 - Supplementary Material-2).

3.4. Combining the results of the model outputs for TYLCV, open field tomato cultivation and B. tabaci for current time and under four climate change scenarios

Overlaying the results for the three species under the current time

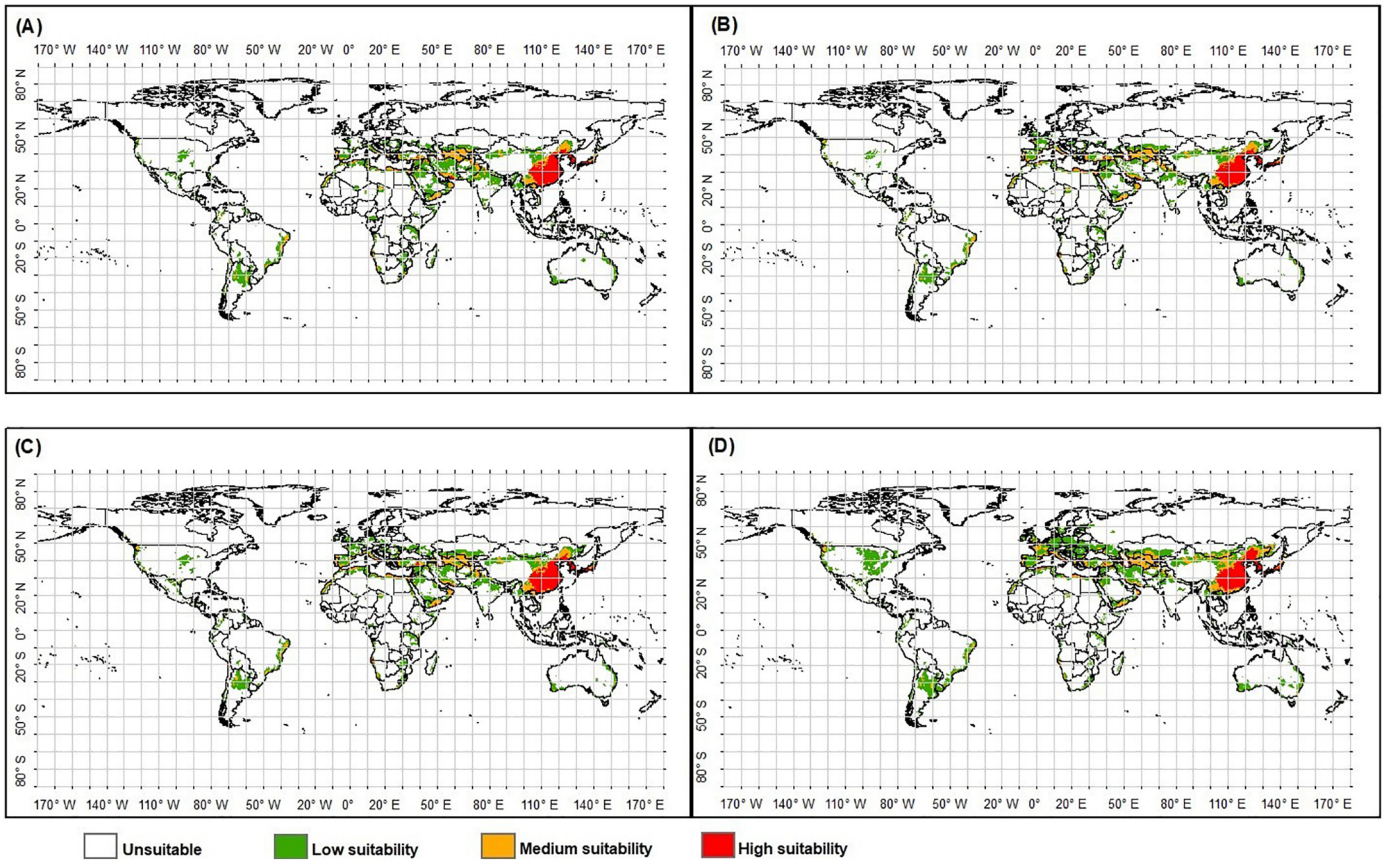

Fig. 3. Habitat suitability under future climatic conditions (2070) for *TYLCV* using the HadGEM2_ES - MaxEnt model running four scenarios (A) RCP 2.6, (B) RCP 4.5, (C) RCP 6.0 and (D) RCP 8.5.

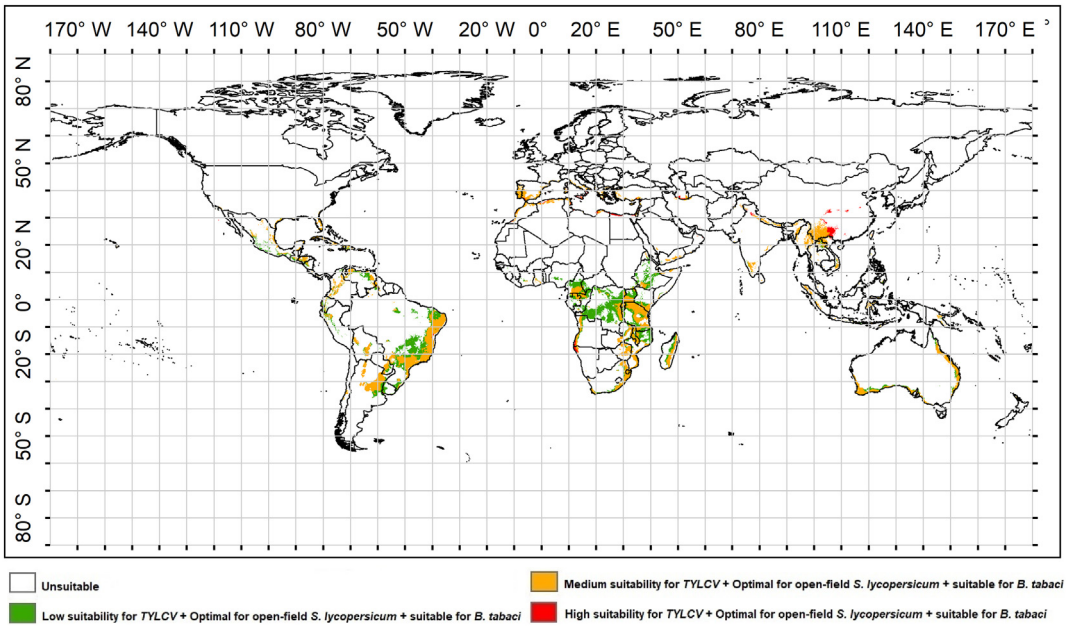
Unsuitable
Low suitability for TYLCV + Optimal for open-field S. lycopersicum + suitable for B. tabaci
Medium suitability for TYLCV + Optimal for open-field S. lycopersicum + suitable for B. tabaci
High suitability for TYLCV + Optimal for open-field S. lycopersicum + suitable for B. tabaci

Fig. 4. Agreement in the MaxEnt model of suitable areas for *B. tabaci* (biotype B and Q) and optimal for *S. lycopersicum* with four risk levels of invasive *TYLCV* under current climatic conditions based on the MTSPS threshold.

shows that some areas in South and Central America, Africa, Mediterranean basin countries, South of China and Australia are under optimal conditions for *S. lycopersicum* and suitable for *B. tabaci* at low (33.5%), medium (62%) and high risk (4.5%) of *TYLCV* (Fig. 4). Overlaying the projection results for the three species shows that some areas in China, Australia, Europe, Africa, and North and South America will be optimal for open field tomato and suitable for *B. tabaci* at low (38%), medium (52%) and high risk (10%) of *TYLCV* until 2070 (Figs. 5, Figs. S20 and S22 - Supplementary Material-2).

According to the four projected scenarios for 2050 and 2070, the

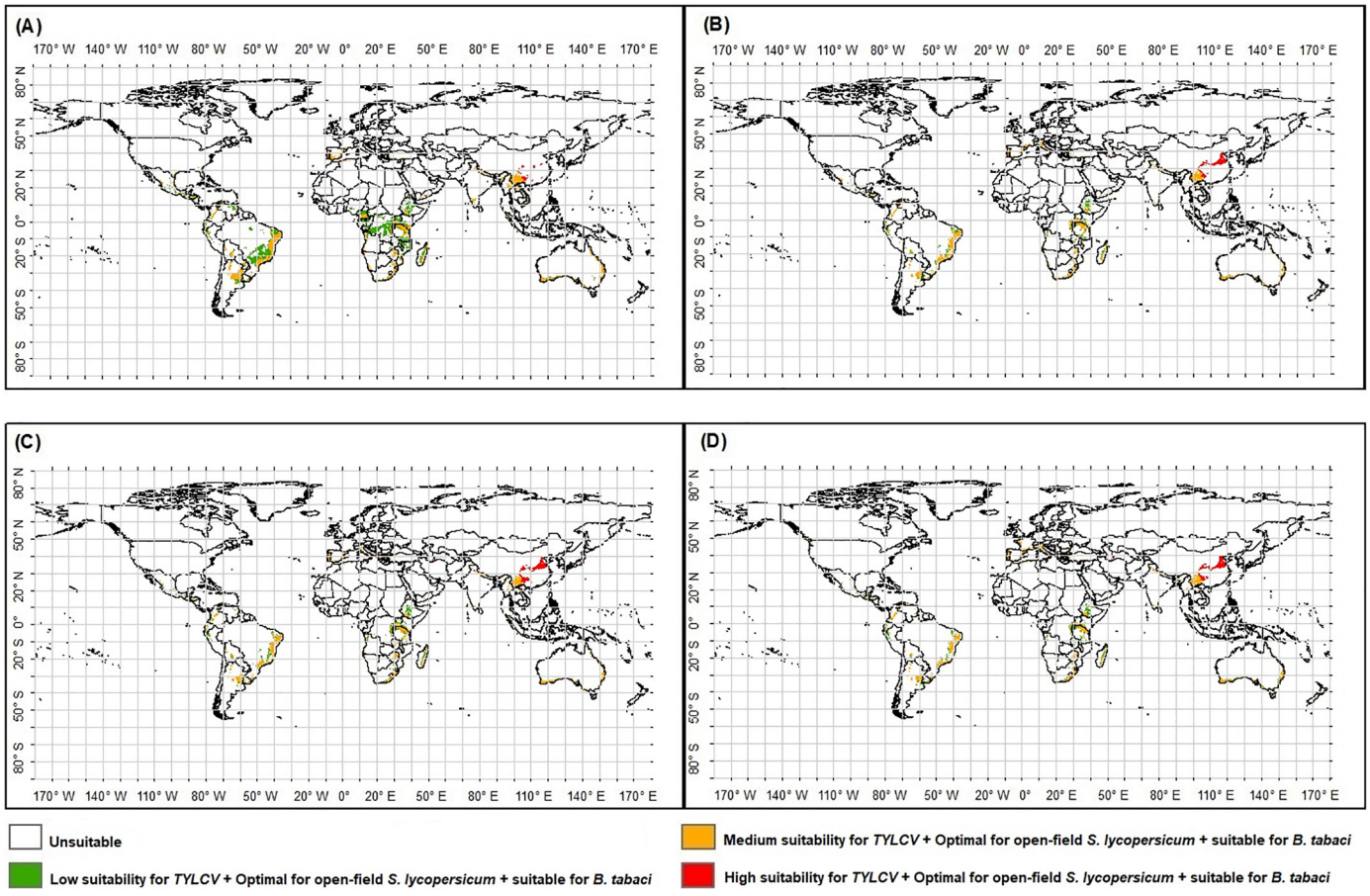
(A)
(B)
(C)
(D)
Unsuitable
Low suitability for TYLCV + Optimal for open-field S. lycopersicum + suitable for B. tabaci
Medium suitability for TYLCV + Optimal for open-field S. lycopersicum + suitable for B. tabaci
High suitability for TYLCV + Optimal for open-field S. lycopersicum + suitable for B. tabaci

Fig. 5. Agreement in the MaxEnt projection of suitable areas for *B. tabaci* (biotype B and Q) and optimal for *S. lycopersicum* with four risk levels of invasive *TYLCV* under HadGEM2_ES running four different scenarios (A) RCP 2.6, (B) RCP 4.5, (C) RCP 6.0 and (D) RCP 8.5 for 2050 based on the MTSPS threshold.

risk of high suitability for *TYLCV* will increase by 111% compared to the current risk level in many locations, such as the United States, northern and northeastern China, southern Kazakhstan and in many European countries. Alternatively, the low and medium suitability risks decrease to 93% and 92%, respectively, compared to the current risk levels in areas of varying suitability in South America (e.g., Argentina and Brazil), Central America, Mexico, Africa, Saudi Arabia, India and Iran. The host *S. lycopersicum* indicates decreases in low, medium and high suitability categories compared to the present at many sites in South and North America, Africa, and in countries, such as Australia, India, Thailand and China. Increased areas are only evident in the low and medium suitability categories and only occur in Europe. High suitability for *B. tabaci* shows increases compared to the current levels in China and Europe but decreases in low and medium suitability in South America, Africa, India and Australia.

Overlaying the results for *TYLCV*, *S. lycopersicum* and *B. tabaci* indicates that most of the countries projected to be optimally suitable for *S. lycopersicum,* as well as suitable for *B. tabaci,* will be under medium suitability for *TYLCV* with a few sites (e.g., South America and Africa) at low risk. The future predictions for the four scenarios show large reductions in the areas with *TYLCV* risk levels, most of them due to the reduction of climatic conditions suitable for the host (*S. lycopersicum*).

4. Discussion

A comparison of the global climate suitability model with the current global distribution of *TYLCV* (Fig. 1A) shows consistency. Climatic conditions suitable for *TYLCV* are projected for many places in the world with low, medium and high suitability areas in Europe, Asia, North Central and South America, and Africa. However, there are some projections in areas in South America, for example, Brazil, where the virus has not yet been reported. Although the climate conditions show medium and high suitability in those areas, the reason for this could be because Brazil basically does not import tomato seedlings, and no infected plants have reached this country, or alternatively due to the extensive use of resistant tomato plants in many sites in the country (Gilbertson et al., 2015; Inoue-Nagata et al., 2016). In case this virus had reached the country but could not establish. We highlight this point because there are so many places on the continent under high risk for *B. tabaci*, which is the insect vector (Fig. 1C), and for that reason, those areas might be under risk from *TYLCV*, since the insect vector is already present. In addition, *TYLCV* was reported for the first time on the continent in 2007 at a location in Venezuela (Zambrano et al., 2007). *B. tabaci* has spread to America, and once the insects have acquired the virus, they are able to spread it to virus-susceptible plants. The introduction of *B. tabaci* in areas never previously reported, or *TYLCV* in areas where *B. tabaci* is already present, can lead to invasion and severe virus outbreaks (Götz and Winter, 2016).

The models presented in this study show a great degree of reliability. The chosen *TYLCV* model produced the lower BIC and AIC_c values, and an 88.7% agreement under AUC with the current modeled global climate and test omission rate at 10% and 0% of 0.1 and 0.02, respectively. All the models performed better than expected at random and show a high validation statistic. The high level of agreement with current *TYLCV* and *S. lycopersicum* distribution confirms the consistency of the models (Fig. 1 A, B).

TYLCV was observed occurring in a wider range of precipitation (7-3146 mm) but most preferably in low rainfall sites with a mean of 890.5 mm (Table 1). The virus may occur in low rainfall areas due to tomato crop irrigation, accounting for the development of the host and

consequently for the viruses. We also observed that *TYLCV* is more likely to occur in areas with high temperatures (Ghandi et al., 2016). High temperatures have been observed to favor virus replication, while low temperatures delay infections and result in only mild symptoms (Ghandi et al., 2016; EFSA, 2014). This is confirmed by the results (response curves) in locations with a high mean annual temperature (Fig. S2).

In our model, we included the occurrences of tomato crops in open field conditions even though, in some regions, tomato does not grow in an open field in all seasons (e.g., north United States). In addition, we noted that the predictions of suitable areas for tomato production were established based on the current climatic thresholds from current commercial cultivars. Currently, tomato plants are introduced in areas where they cannot grow without aid. However, the production of tomatoes may become possible due to the development of new cultivars resistant to high temperatures and the production of tomatoes in protected areas when temperature and other climatic conditions are controlled. Although tomato cultivation is still undertaken in the open field, the current trend in tomato cultivation increasingly favors net houses or closed greenhouses. In both systems, the temperature can be controlled by proper ventilation or air-conditioning, thus altering the microclimate of the crops. It should be noted that modeling studies cannot take either of these conditions into account.

TYLCV dynamics may be influenced negatively at high temperature since the current *B. tabaci* biotypes exhibit a lower fertility than at temperate climates (Tsueda and Tsuchida, 2011). New emerging biotypes, much more resistant to heat, may be selected by increased temperatures. It is known that the biotypes of *B tabaci* are very dynamic and one may replace another within a few years (i.e., biotype B replacing A in the USA, and biotype Q replacing B in the Middle and far east) (Al-Shehi and Khan, 2013; Gnankine et al., 2013; Ramos et al., 2018).

The climatic conditions for *TYLCV* found in this study match the ideal conditions for tomato open field cultivation. Tomato crops have an optimum temperature range from 20 to 27 °C, as well as poorer development in regions with high annual precipitation (> 1800 mm) (FAO, 2007). All the climatic factors used in this study indicate that *TYLCV* has climatic requirements similar to the host, further confirming the quality of our model in predicting *TYLCV* occurrence in most locations where tomato is cultivated in open field conditions (Fig. 1, S3, Table S1 - Supplementary Material-2). Climatic conditions, such as suitable temperatures may, therefore, contribute to the potential invasion of *TYLCV* in regions of open field tomato where the presence of the virus has not yet been reported, thus compromising the tomato productivity in many important tomato production regions.

Although *TYLCV* may establish across a wide thermal range, the virus is affected by global temperature changes (Figs. 2, 3, Figs. S4, S5, S6 and S7 - Supplementary Material-2). If the increase of the temperature predicted in the HadGEM2-ES, MIROC5 and CCSM4 models occurs, it may extend the limits for occurrence, as well as limiting the growth and development of the host, and affect the insect vector distribution. The *TYLCV* virus requires the interaction of a susceptible host and environment that is favorable for disease development. This indicates that the virus is dependent on the survival of the host, *S. lycopersicum*, a species that shows great sensitivity to extreme environmental conditions, especially temperature. In this context, studies have reported that temperature (high or low) may affect the suitability of the host (host resistance) and the interaction between the host and virus (Anfoka et al., 2016; Canto et al., 2009; Ghandi et al., 2016). Our model results for all the scenarios in the future indicated that greater reductions in suitability for tomato crops are predicted even more than for *TYLCV*. The virus can establish in an area even without the vector and spread there through seeds. However, without the vector, its establishment can be less likely if seeds are not taken from the plants produced, but new crops are always started form new seeds coming from somewhere else. The presence of the vector ensures that the virus spreads between the host plants and may also end up in weeds and be preserved in the field.

According to the projected scenarios for 2050 and 2070, many global regions, such as in South America (e.g., Argentina and some areas along the coastlines of Brazil), North America (the United States), Africa (along the coastlines of the continent) and south of Europe are projected to remain suitable for *TYLCV* (Figs. 2, 3, Figs. S4, S5, S6 and S7 - Supplementary Material-2). Similarly, suitability will be maintained in many regions for tomato cultivation (e.g., along the coastlines of Brazil, southern Europe and West Africa), as well as for *B. tabaci* (e.g., along the coastlines of southern, southeastern and northeastern Brazil and southern and eastern Australia) (Figs. S8, S9, S10, S11, S12 and S13 - Supplementary Material-2). However, the model demonstrates that this suitability for *TYLCV* will increase for 2050 and 2070 in a northern direction in Europe (Spain, Italy, France, Germany and Hungary), Asia (northern China) and North America (some sites in the United States). Tomato cultivation suitability will increase in a northern direction in European countries (Spain, Italy, France, Germany and Hungary) but decrease in Asia (India) and Africa. In general, the suitability for *TYLCV* will decrease for 2050 and 2070 for South and Central America, Africa, Asia (India) and Iran (Figs. 3, Figs. S6, S7, S17, S18 and S19- Supplementary Material-2) and for the host in all the continents (America, Africa, Asia, Europe, and Oceania) (Figs. S14, S15, S16, S17, S18 and S19 - Supplementary Material-2). While the differences between the scenarios are few for all three species (virus, host and vector), RCP 8.5 shows larger areas under low suitability for *TYLCV* (e.g., the United States, northern Europe and northern China) compared to the others. The fact that RCP8.5 projects the greatest mean global temperature to increase and is the only scenario assuming the continuation of greenhouse gas emission, increases throughout the 21st century may explain these larger areas (Meinshausen et al., 2011). For tomato open field cultivation, both RCP 6.0 and RCP 8.5 show larger decreases of suitable regions (e.g., Africa, South America, Australia and China) than the general decrease for 2050 and 2070 (Figs. S14, S15, S16, S17, S18 and S19- Supplementary Material-2). For *B. tabaci* suitability, RCP 8.5 again indicates larger decreased areas (e.g., Africa and India), but an increase in some areas (e.g., the United States and Europe) compared with the general maintenance of suitability for 2050 and 2070 (Figs. S7 and S14-Supplementary Material-2).

Our models do not take into account the fact that most cultivars are now tolerant to *TYLCV*. This means that there are several orders of magnitude less virus in the plants than in susceptible cultivars. As a result, the whiteflies pick up much less virus, and the amount of the infection decreases (Legarrea et al., 2015). It is possible that *TYLCV* will disappear on tomato in the future. The virus will still exist but on an alternative host such as weeds (Vallad et al., 2015). Alternatively, new variants may occur, which will break tolerance.

Combining the results for the three species shows that some areas in China, Australia, Europe, Africa, and North and South America will be optimal for open field tomato and suitable for *B. tabaci* with low, medium and high risk of *TYLCV* current and until 2070 (Figs. 4, 5, Figs. S20, S22- Supplementary Material-2). According to the four scenarios projected, the risk levels (low or high suitability) for *TYLCV* will increase when compared to the current levels in many regions, such as the United States, northern and northeastern China, southern Kazakhstan and northern Europe. However, a decrease in the risk is shown in some areas with different suitability levels in South America (e.g., Argentina and Brazil), Central America, Mexico, Africa, Saudi Arabia, India and Iran. The suitable levels (low, medium and high suitability) for *S. lycopersicum* will decrease when compared to the current levels for many regions in South and North America, Africa, and in countries, such as Australia, India, Thailand and China, while some will increase (low and medium) suitability in Europe. The overlaying results for *TYLCV*, *S. lycopersicum* and *B. tabaci* indicate that most countries that are projected to be optimally conducive for *S. lycopersicum* and suitable for *B. tabaci* will be under medium suitability for *TYLCV* with few localities at

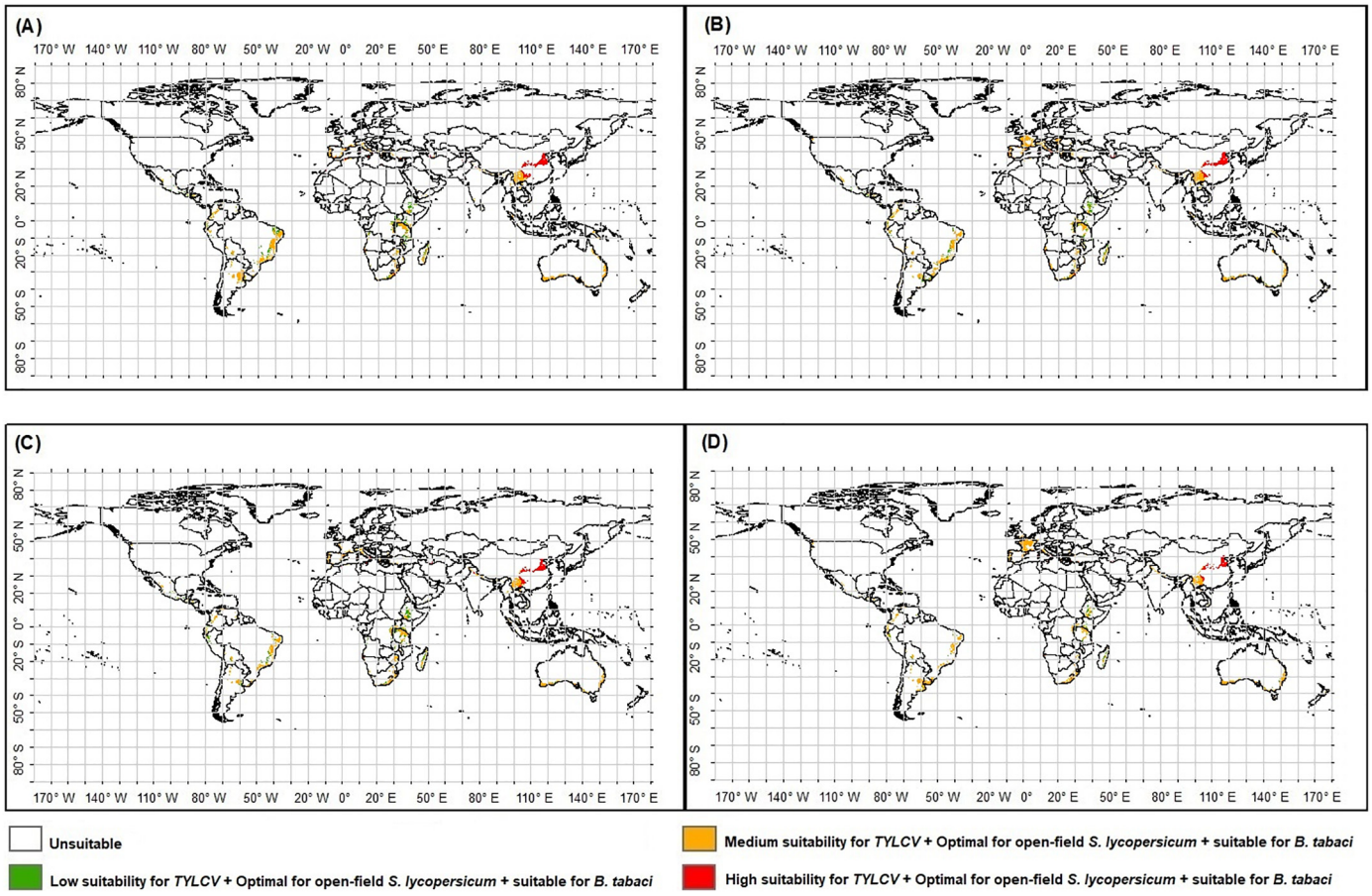
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Fig. 6. Agreement in the MaxEnt projection of suitable areas for *B. tabaci* (biotype B and Q) and optimal for *S. lycopersicum* with four risk levels of invasive *TYLCV* under HadGEM2_ES running four different scenarios (A) RCP 2.6, (B) RCP 4.5, (C) RCP 6.0 and (D) RCP 8.5 for 2070 based on the MTSPS threshold.

low risk (Figs. 4, 5, 6, Figs. S20, S21, S22, and S23- Supplementary Material-2). The future predictions for the four scenarios show large reductions in the areas of the *TYLCV* risk levels. The primary reason for the significant decrease in the total area conducive for open field tomato is an overall reduction in suitable climatic conditions (Figs. 5, 6, Figs. S20, S21, S22 and S23- Supplementary Material-2).

5. Conclusions

Our study shows that climate change may affect the *TYLCV* global distribution, as well as that of its host, *S. lycopersicum*, and vector, *B. tabaci*. The methods utilized in this study are relevant and can be applied to other agricultural crops and to manage other viruses (i.e., Begomovirus). The results of the climate change for two different species, using the HadGEM2-ES, MIROC5 and CCSM4 models under four different scenarios, provide an indication of potential global climatic changes and their impact on tomato production. Globally, in all the GCMs presented in this work, there are areas at increased risk of *TYLCV*. Some will maintain current risk levels, while the risk will decrease in others. In all predictions, there are consistent risk levels and agreement between the ensemble outputs under the three GCMs and the four RCPs. The same regions in all continents present high similarities in terms of suitability for the three species. Some regions are predicted to become optimally conducive for open field *S. lycopersicum*, as well as suitable for *B. tabaci*, with different risk levels of *TYLCV*. For 2050 and 2070, most areas with optimal conditions for *S. lycopersicum* and suitable for *B. tabaci* will be under medium suitability for *TYLCV* with few localities at low risk. Future research could consider the impact of nonclimatic factors under MaxEnt modeling and overlay additional layers to refine the results to a more extensive range of environmental scenarios and locations. To prevent the infection or spread of *TYLCV,* it is critical to control the vector but also new strategies to avoid seed transmissions are needed. Our results may be useful to design strategies to prevent the introduction and establishment of *TYLCV* in some countries in South America, in which the occurrence of the virus has not yet been reported, as well as to promote greater investment in pest management programs, especially in areas that are becoming more suitable for the host but are under medium and high risk for the virus.

Author contributions

RSR and MCP conceived and designed the research. RSR acquired and analyzed the data. RSR wrote the manuscript with help from LK and MCP. LK and FS made critical revisions (providing language help and writing assistance). LK and MCP made critical revisions and approved the final version. All the authors reviewed and approved of the final manuscript.

Acknowledgements

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Conflict of interest

The authors declare that they have no conflict of interest.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.agsy.2019.03.020.

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